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ORIGINAL ARTICLE

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Combining motions into complex displays: playbacks with a robotic lizard

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Abstract Complex displays composed of multiple, seemingly independent, units can result from sexual selection for increasingly variable, but redundant, displays and from potentially opposing selective pressures imposed by use of the display in multiple contexts. Our playback results support the latter, multireceiver hypothesis by confirming that two aspects of the sagebrush lizard headbob display (number of headbobs and use of display-specific body postures) are independently-meaningful components that are interpreted differently by different receivers. Male receivers use species-typical body postures to distinguish between aggressive and broadcast forms of the display, whereas female receivers are more attentive to the number of headbob motions, using these to distinguish male courtship from a challenge from a female competitor. Thus, display components are likely subject to different selective pressures and the display as a whole is evolving in response to a complex selective regime. Our example differs from other complex signals that have been considered in that both display elements involve dynamic motions (turned on and off by the display producer) as opposed to static signal elements (e.g., color, size). In addition, we found evidence that display structure is highly malleable, and that lizards both produce and respond to artificial displays that violate syntactic rules identified from field observations. Finally, our experiments demonstrate that a robotic lizard can be used effectively in playback studies of visual display behavior in lizards.

Keywords Behavior · Communication · Evolution · Lizard · Robot playback · *Sceloporus graciosus* · Sexual selection

Introduction

Most animal communicative signals are composite structures combining multiple elements, sometimes even crossing sensory modalities. For example, the snapping shrimp ‘open chela’ display combines chemical and visual elements into a single multimodal display (Hughes 1996). Male red-collared widowbirds add a highly conspicuous red chest patch to a long train of tail feathers during the courtship season (Andersson et al. 2002). Primate copulation calls seem to be behaviorally and evolutionarily linked to the dramatic visual signal of female sexual swellings (Maestripieri and Roney 2005). Composite displays can result from sexual selection via female choice if costs to the receiver are low or if receiver preferences fluctuate over time (Pomiankowski and Iwasa 1993; Iwasa and Pomiankowsk 1994). We term this the “Low Cost Redundancy Hypothesis”. In contrast, the “Multi-Receiver Hypothesis” suggests that multiple design elements evolve when aspects of the signal are subjected to different forms of selection in different contexts (e.g., courtship and territorial aggression – Marchetti 1998; Andersson et al. 2002). Apparent complexity may also be superficial, representing features that seem separate to a human observer, but which are tightly genetically linked and actually evolving as a single unit or ‘trait’. Herein, we use a playback approach to partition a complex visual display into meaningful units and to distinguish whether elements function in concert or as separate entities in different signal contexts.

Electronic Supplementary Material: S1. Movie clip of the robotic lizard producing a species-typical headbob display as in Fig. 1a.

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We focus on the lizard headbob display system, where the structural complexity of visual signals has been shown to vary consistently among species, populations, individuals, and sexes (e.g., Ferguson 1970; Carpenter and Ferguson 1977; Jenssen 1977). Headbob displays are produced in a variety of contexts, including territorial defense, broadcast, courtship (e.g., Martins 1993; Decoury and Jenssen 1994), appeasement (Martins and Lacy 2004), and anti-predator situations (Leal 1999). Describing complex motor patterns such as headbob displays can be done in an infinite number of ways. Although some researchers have divided up the display system based on putative function and the contexts in which the displays were produced (e.g., 'assertion' and 'challenge' displays – Carpenter 1967), a plethora of structural classifications have also been proposed. For example, Carpenter (1978b; and later Martins 1991, 1993) emphasized the importance of body postures, patterns of leg extension and orientation. Others (Jenssen 1975, Jenssen and Rothblum 1977; Rothblum and Jenssen 1978; Bels 1986; Font and Kramer 1989) have persuasively applied more statistical approaches, measuring the amplitude and duration of each headbob and using multivariate statistics to identify display types. Most recently, researchers have applied Fourier analyses (Fleishman 1988) and optic flow algorithms (Peters et al. 2002) to quantify the motion characteristics making up lizard visual displays. Combination of display components seem to be regulated syntactically, making the headbob display system as structurally rich as those commonly described for birds and mammals (Martins 1994).

We focus on two display components that seem to convey similar, if not identical, information: 1) the use of display-specific body postures and 2) the total number of up-and-down motions or 'headbobs'. Although lizard headbob displays traditionally have been considered to be species-typical (e.g., Carpenter and Ferguson 1977), display-specific body postures ('modifiers', *sensu* Jenssen 1971 – e.g., gular extension, lateral flattening, arched back) are variable in many iguanid species and have long been viewed as the main feature distinguishing highly aggressive, close range displays ('challenge' or 'fullshow') from the broadcast ('signature' or 'assertion') displays typically viewed at a distance as an animal patrols its territorial boundaries. Although most descriptions of the species-typical nature of lizard headbob displays focus on the detailed amplitude, timing, and number of up-and-down motions in the headbob pattern (e.g., Display-Action-Pattern or 'DAP' graphs; see Fig. 1), these too are variable within a species. For example, Carpenter (1978a) labels about half of the 42 species described in his seminal monograph of *Sceloporus* lizard displays as being "indeterminate" displayers, with variable numbers of headbobs in their displays. Similarly, *Anolis carolinensis* displays have been described as coming in three forms (Types A, B, and C) which vary in which and how many headbobs are employed (Decoury and Jenssen 1994). The total number of headbobs seems to be positively related to display intensity, with more headbobs being used in displays that are directed towards specific individuals at short distances (Martins 1993; Decoury and Jenssen 1994, Lovern and Jenssen 2001), and in displays produced after the animal has run longer distances (Martins 1993). Variation in both body postures and total number of headbobs can also be used to distinguish individuals, sexes, and populations (e.g., Ferguson 1970; Martins 1993; Martins et al. 1998).

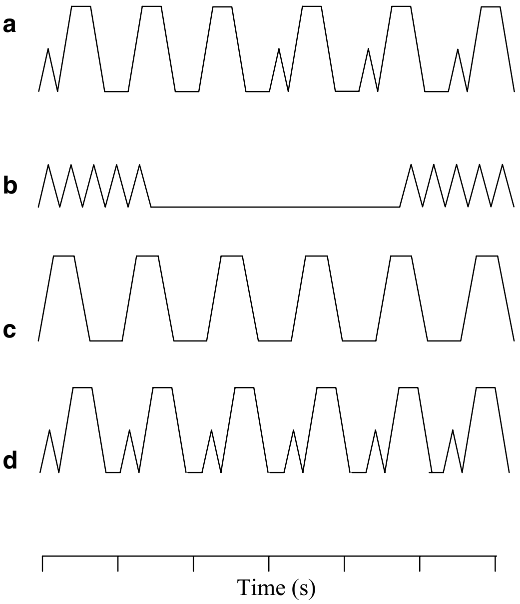

Fig. 1 Display-Action-Pattern graphs (*sensu* Carpenter and Grubitz 1961) describing the displays performed by the robotic lizard. The x-axis represents time, in seconds. The y-axis describes the relative height of the model's head. **a** The typical sagebrush lizard aggressive display (ABBCCC; 'assertion', 'signature' or 'broadcast' display), which was used as the headbob sequence in Experiment 1 and as one of the 'natural' displays in Experiment 3. For the 'long' signal form in Experiment 2, a B bob was deleted and a terminal C bob added (ABCCCC), while the 'short' form had the same initial components but retained only one C bob (ABC). **b** A typical shudder display (SSSSS___SSSSS) performed by males and usually directed towards females during courtship and used as the second 'natural' display in Experiment 3. **c** A series of uninterrupted single headbobs (BBBBBB) and **d** double headbobs (CCCCCC). These latter two display sequences have never been observed in the field for this species (Martins 1991, 1992, 1993) and were used as the 'artificial' displays in Experiment 3

The above evidence is based purely on structural analyses of observed displays. Playback experiments are needed to determine whether signal components are perceived as separate elements by display recipients, and/or whether components function differently in different contexts. Fortunately, visual playback experiments have become increasingly common and have been applied to a taxonomically diverse range of taxa; from crustaceans to primates (see Ord et al. 2002 for review). Despite differences in the visual system of lizards and humans, video and computer animation playbacks have proven to be a particularly attractive option, allowing unprecedented manipulation of the temporal and physical attributes of a stimulus (e.g., Ord and Evans 2003; Peters and Evans 2003). Whereas it takes a great deal of time and expense to create video and computer stimuli, technology is currently available to build inexpensive, precisely-controlled robotic models that allow rapid and flexible variation of the stimulus being presented. Robotic models have been used effectively with frogs (Narins et al. 2003), birds (Patricelli et al. 2002) and lizards (Thompson 2002), offering another promising approach. Herein, we use a robotic model to test the behavioral response of southern sagebrush lizards, *Sceloporus graciosus*, to variation in display components and to measure the degree to which these components function independently.

Our experiments begin with a series of calibration trials that compare the response of subjects to a live lizard stimulus and the robotic model. In a second experiment, we manipulate the total number of headbobs and the use of body postures and measure the effect on the behavioral response. In a third experiment, we focus on the details of the headbob display structure, comparing responses to headbob displays which vary in the types and proportions of up-and-down motions.

Methods

Subjects

Subjects were 26 male (53–62 mm snout-vent length (SVL); 8.3–10.9 g) and 24 female (54–61 mm SVL; 6.7–10.6 g) lizards caught in the field at Table Mountain in the Angeles National Forest of southern California. Experimental trials were conducted in April and May 2003. Adult lizards had been living in our captive colony at Indiana University, Bloomington for about 1 year before the start of our experiments, undergoing a 6-week period of hibernation in late December and January, and being housed in standard conditions (5-gallon aquaria, 10:14 light:dark cycle, sand substrate, heat gradient, and *ad libitum* feeding). Although southern sagebrush lizards in the field are just beginning the mating season in April and May, our captive colony had been exhibiting male courtship behavior and decreased female territorial behavior for approximately 1 month (consistent with what is typically seen during middle-to-late summer in the wild; Martins 1993).

Testing and scoring procedures

Each experiment was completed in a 4–7-day session (Experiment 1: April 10–13; Experiment 2: April 23–29; Experiment 3: May 16–19). Trials were conducted during the peak daily activity periods, at least 2 h after colony lights had been turned on. To maximize statistical power, we designed experiments consisting of four treatments grouped into two factors, exposing each animal to all four treatments in random order (never more than one treatment per day). We thus conducted a total of 200 trials each in Experiments 1 and 2 (26 males and 24 females), and 100 trials in Experiment 3 (25 males only).

Each treatment began by moving the animal's home aquarium into a testing room, where it was placed beside a second aquarium containing the experimental stimulus (see below). The adjacent sides of the two aquaria were visually separated by a cardboard divider. The researcher turned on the robotic lizard (when used) and a camcorder directed at the subject (Panasonic AG-188) and then left the room. After 2 min, the divider separating the subject and stimulus was removed remotely (by pulling a string from an adjoining room), allowing the subject animal visual access to the experimental stimulus through two panes of aquarium glass. The behavior of the subject animal was recorded for 8 min for Experiments 1 and 2, and 18 min in Experiment 3.

Videotapes were scored by a single observer (EPM) who recorded continuously all behavioral incidences (e.g., locomotion, headbob displays, tongue flicks, and head turns), the horizontal position of the subject in the aquarium (in cm from the stimulus), and the subject's orientation with respect to the stimulus (dividing the space around the lizard's head into 90° sections: front, right, left, and back). Data were then processed through a Microsoft Access database programmed to calculate frequencies, proportion of time spent oriented towards the stimulus, and average distance from the stimulus.

Statistical analyses

Sagebrush lizards are relatively sedentary animals and most subjects moved about little during the trial. We thus analyzed each experiment twice, using all of the data first and then running each analysis again using data only from the subset of trials in which the subject moved at least once. For Experiments 1 and 2, we analyzed data for males and females separately.

Because of the artificial laboratory setting in which this experiment was conducted, we focus our conclusions on the abilities of animals to distinguish among treatment conditions and adopt a cautious approach to interpreting the behavioral details of their responses. We began each analysis by using Principal Components Analysis (PCA) to reduce the behavioral measures from each experiment into a smaller number of meaningful composite variables. The effect of the two treatment factors on the composite variables in each experiment was then tested in a two-way MANOVA (multivariate analysis of variance) including an interaction term. We applied natural log transformations to behavioral counts and distance measures (before running the PCA) after noting from residual plots that they improved the normality and homogeneity of variances in the MANOVAs. We further analyzed in detail the headbob displays produced by animals in each trial, comparing the number of displays and display structure (i.e., number and type of headbobs) across treatments. All statistical analyses were conducted using SPSS for Windows (2002).

Experimental treatments

Experiment 1 – apparatus calibration

In this experiment, we compared the response of subjects to: 1) a live lizard stimulus (alternating among three male lizards that were not used as subjects in any of the experiments); 2) an empty aquarium; and 3) the robotic lizard producing a species-typical display (ABBCCC; Fig. 1a and S1). The robotic stimulus consisted of a latex dummy attached to a stepper motor (15° linear actuator, HSI 46000 series; Hayden Switch & Instrument, Inc) controlled by a compact integrated driver (MicroLynx4, MX-CS100-400; Intelligent Motion Systems, Inc). The model was attached directly to the stepper motor, which was hidden below the dummy lizard in a small cardboard box, while the controller was out of view from the subject behind the tank. A movie clip of the robotic lizard is available in the supplementary materials (S1). An identical cardboard box served as a low perch in the presentation tank of the live animal (and the empty tank control). In addition to the empty cage control, we added a fourth treatment intended to simulate a general novel disturbance. Subjects in our pilot studies reacted strongly to any lizard-like stimulus, including nonmoving lizard-like shapes and a red cube producing lizard-like pushup displays. Thus, to simulate a more general, nonlizard-like disturbance, we chose a novel sound. Specifically, for our fourth treatment, we removed the rubber lizard from above the box housing the stepper motor, but left the apparatus running to produce the same mechanical noise as when producing the species-typical display. Subject animals could clearly hear the sound, but were unlikely to attribute it to another animal.

These four treatments can be summarized as two factors with two states each. The first factor was 'live/robot', scored as 0 for the live lizard and empty aquarium stimuli, and as 1 for the mechanical lizard producing a headbob display and for the sound of the apparatus without the rubber model. The second factor was 'moving/nonmoving', scored as 0 for the live lizard and mechanical headbob display conditions, and as 1 for empty aquarium and mechanical sound treatments. The interaction term in our MANOVAs tests for differences between live and robotic lizard treatments, scaled first with respect to the control treatments.

Experiment 2 – body posture and bob number

In Experiment 2, we used the robotic lizard in all four treatments to test the relative effects of a) species-typical body postures and b) the total number of headbobs in the display. To test the effects of species-typical body postures, we used the lizard model from Experiment 1 which exhibited a 'flat' posture typical of animals in the field while performing long-distance broadcast or short-distance courtship displays (Martins 1993), and created a second 'stilted' latex model of a lizard with all four legs extended and exhibiting lateral compression, arched back, and gular extension. This combination of leg extension and body posture is most commonly exhibited in sagebrush lizard aggressive displays (Martins 1993). Although both 'flat' and 'stilted' models were painted with a blue belly (as perceived by a human observer), we made no attempt to match color spectra to that of a live animal (see Stuart-Fox et al. 2003), focusing instead on the posture. To test the effects of total headbob number, we had both 'flat' and 'stilted' lizard models produce two forms of headbob displays: a short form of the display (ABC) and a longer form (ABCCCC, Fig. 1), in all possible combinations. Both sequences are used commonly by lizards from this population in the field. Videotaped images of these treatment stimuli are available in the supplementary materials (S1).

Thus, the four display types used in this experiment were: 1) short, stilted; 2) short, flat; 3) long, stilted; and 4) long, flat. At short distances comparable to those employed in our experiment, display types 2 (short, flat) and 3 (long, stilted) correspond to those used primarily between females and males (respectively) during aggressive territorial disputes (Martins 1993). Display type 2 (short, flat) is also similar to Display type 1 (short, stilted) in being used commonly as Broadcast ('assertion' or 'signature', sensu Stamps and Barlow 1973) displays, typically viewed from much longer distances (>1 m) than allowed by our study. Display type 4 (long, flat) is comparable to the courtship displays directed by males towards females from short-distances (Martins 1993). Hence, our MANOVA test for a main effect of 'short/long' might also be interpreted as a comparison of responses to Broadcast and female aggression (display types 1 and 2) with responses to male aggression and courtship displays (display types 3 and 4). The main effect for 'flat/stilted posture' compared response to Broadcast and male aggression (display types 1 and 3) with response to female aggression and courtship displays (display types 2 and 4). Finally, the MANOVA interaction term compared response to aggressive displays (display types 2 and 3) with response to Broadcast and Courtship displays (display types 1 and 4).

Experiment 3 – Headbob type and pattern

The sagebrush lizard headbob display combines single up-and-down motions with 'double bobs', in which the head moves up-and-down two times in rapid succession (the first headbob being typically of much lower amplitude than the second; Fig. 1a). In Experiment 3, we varied the fine structure of the headbob display by varying the number and timing of single (B) and terminal double (C) bobs in the display. In all cases, we used the rubber model of a lizard in a 'flat' or resting posture. As in the other experiments, one treatment (1: 'signature') was the species-typical headbob display (ABBCCC) which combines single (B) and double (A and C) headbobs (Fig. 1a, and c; bobs are identical in form but distinguished from each by whether they proceed or follow single bobs). In a second treatment involving a naturally-occurring display (2: 'shudder'), we presented lizards with a display commonly used by male lizards during courtship interactions. The 'shudder' display consists of a series of rapid, low amplitude up-and-down motions interspersed with lengthy pauses (SSSSS____SSSSS; Fig. 1b), and usually produced while the animal is moving from one place to another. Although the shudder is a common display for this population and species, it is almost always directed by males towards females during courtship, and hence probably appears odd when directed by a stationary robot to the male subjects of this experiment. We then created two artificial displays. In the third treatment (3: ‘all singles’), we presented subjects with a series of uninterrupted single headbobs (BBBBBB; Fig. 1c), whereas in the fourth treatment (4: ‘all doubles’), we presented a series of double headbobs (As and Cs as produced by our robotic lizard are identical; we refer to this display arbitrarily as CCCCCC; Fig. 1d).

Again using a two factor design, we grouped treatments into naturally-occurring (signature and shudder; ABBCCC and SSSSS) versus artificially-constructed displays (all singles and all doubles; BBBBBB and CCCCCC). For the second factor, we compared the response to displays that did (ABBCCC and CCCCCC) or did not (shudder display and BBBBBB) include double bobs in their sequence. The interaction term offers a scaling control by testing for differences in response to ABBCCC and BBBBBB vs. SSSSS and CCCCCC displays.

Results

Experiment 1 – Apparatus calibration (robot versus live)

Using Principal Components Analysis (with Varimax rotation and Kaiser normalization), we successfully constructed four composite variables that described the response behavior in sensible ways while explaining most (75%) of the variance in the data (Table 1). The first of these (PC 1) summarizes variation in general activity levels and included total distance moved during the trial, summed count of chemical behavior (tongue flicks, head turns, defecation, jaw, cloacal and side rubs), total time spent engaging in high intensity locomotion, and the summed count of ‘other’ behavior (including eating, drinking, digging, moving, scratching, and twitching). The second axis (PC 2) summarized variation in visual display behavior (duration and number of headbob and shudder displays), while PC 3 and PC 4 described attention to the stimulus. Specifically, PC 3 combined the average distance from the stimulus and the extra proportion of time spent orienting towards rather than away from the stimulus (time spent facing directly towards the stimulus minus time spent facing directly away from the stimulus divided by the total time), whereas PC 4 was associated with laterality (the extra time spent observing the stimulus from the right eye rather than the left).

Individual subjects varied greatly in the degree of behavioral response with some animals moving about their home cages frequently and interacting with the stimulus whereas others remained entirely still throughout the trial. In 54 of 200 trials, the subject animal did not move at all. There was no sex difference (exactly 50% of the 54 trials involved male subjects) and the 54 trials were roughly evenly distributed among the four treatment types (χ^2=2.6, df=3, p=0.5). Thus, our results did not depend substantively on whether we analyzed behavior of 146 or 200 trials, and are reported below only for the full 200.

The response of male subjects to the robotic lizard was generally similar to that observed towards a live animal and significantly different from that elicited by the two control treatments (empty cage and mechanical sound). This was confirmed by a significant effect of ‘moving/nonmoving’ in the MANOVA (F=5.6, df=4, 96, p<0.0001) and

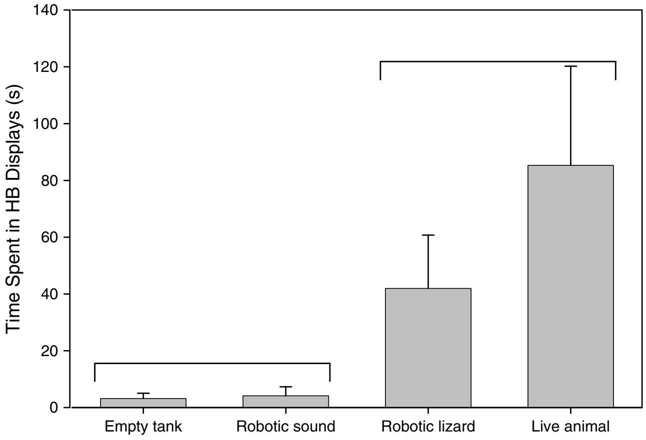

Fig. 2 A comparison of time male subjects spent producing headbob displays to different treatment stimuli. This measure was combined with other measures of visual displays in PC2, and yielded a significant effect for ‘moving/nonmoving’ (robot/live animal versus empty tank/no robot) in MANOVAs. An interaction effect which tests for a difference between responses to robotic and live stimuli was not statistically significant. See Table 2 and text for details

Table 1 Loadings of behavioral measures onto four primary principal components, using data from male subjects in Experiment 1 and a Varimax rotation

Variation explained	Principal components			
	PC 1 (29%)	PC 2 (22%)	PC 3 (14%)	PC 4 (10%)
Ln (distance moved in cm)	**0.93**	0.08	−0.00	0.10
Ln (total “other” behavior)	**0.89**	0.13	0.08	0.00
Ln (total chemical behavior)	**0.86**	0.09	−0.01	0.03
Ln (time in intense locomotion)	**0.57**	0.33	0.20	−0.13
Ln (total number of visual displays)	0.23	**0.91**	0.04	0.01
Ln (time doing headbobs)	0.21	**0.92**	0.04	0.02
Ln (time doing shudders)	0.01	**0.62**	0.10	−0.01
Percent time orienting towards	−0.06	0.04	**0.85**	−0.01
Average distance from stimulus	−0.18	−0.13	**−0.76**	−0.01
Percent time looking from right	0.03	0.02	0.00	**0.99**

Loading of principal components axes for female data and from Experiments 2 and 3 were very similar, with the same variables loading primarily onto the same axes, and values falling within 0.05 of those in the table

Table 2 *F* and Adjusted R^2 values from Multivariate Analyses of Variance (MANOVAs)

	Activity PC 1	Visual displays PC 2	Towards PC 3	From right PC 4	All
Experiment 1: Males (104 trials; 26 males):					
Intercept	0.3	6.0*	0.0	0.1	1.6
Interaction	0.5	0.8	2.8	0.0	1.0
Live/robot	3.2	3.3	0.8	0.2	1.7
Moving/nonmoving	0.5	12.4**	4.0*	4.3*	5.6**
Adjusted R^2	1.3%	11.8%	4.3%	1.5%	
Experiment 1: Females (96 trials; 24 females):					
Intercept	0.3	25.3*	0.0	0.1	6.5*
Interaction	1.3	0.3	0.2	0.0	0.3
Live/robot	2.0	0.2	0.3	0.0	0.7
Moving/nonmoving	0.1	1.5	0.7	0.2	0.8
Adjusted R^2	0.4%	0.0%	0.0%	0.0%	
Experiment 2: Males (104 trials; 26 males):					
Intercept	0.1	15.2**	0.2	0.0	2.4
Interaction	0.5	1.7	1.1	0.5	0.8
Short/long sequence	0.5	1.9	0.3	0.4	0.7
Flat/stilted posture	7.3**	1.8	0.0	1.4	2.9*
Adjusted R^2	6.1%	0.3%	1.6%	0.6%	
Experiment 2: Females (96 trials; 24 females):					
Intercept	0.2	15.7**	0.2	0.0	81.0*
Interaction	0.5	0.0	0.0	0.5	0.4
Short/long sequence	0.1	0.1	4.5*	0.0	1.9
Flat/stilted posture	0.0	0.0	0.4	0.2	0.2
Adjusted R^2	2.5%	0.8%	1.5%	2.1%	
Experiment 3: Males (100 trials; 25 males):					
Intercept	0.0	0.0	0.0	0.0	0.0
Interaction	0.0	0.2	0.3	0.8	0.6
Natural/artificial sequence	0.1	0.3	0.3	0.0	0.1
Double/single bobs	0.3	0.6	1.7	0.2	0.7
Adjusted R^2	0.0%	0.0%	0.0%	0.0%	

*significantly greater than 0 at the $\alpha = 0.05$ level

** significantly greater than 0 at the $\alpha = 0.01$ level

nonsignificant effects for the other main factor and the interaction term ($p > 0.05$, Table 2). Male subjects produced visual displays (PC2) in response to both the live animal and the moving model, but only rarely did so in response to the two control treatments (Fig. 2). Male subjects also paid somewhat more attention to both live and moving robotic lizards (means = 15% of trial time [SE = 12.1]) than to controls (7% [SE = 11.4]). Males both displayed (Fig. 2) and moved less during the robotic lizard trials (mean displacement = 11 cm [SE = 3.8]) than during control or live animal trials (mean displacement = 31 cm [SE = 8.4]), but the MANOVA interaction term, which tests these differences after scaling to variability in the controls, was not statistically significant (Table 2).

Female subjects produced considerably less measurable behavior than did males during this experiment and MANOVAs considering the impact of 'moving/nonmoving' and 'live/robot' on female behavior found no significant differences ($F < 0.8$, df=4,84, p=0.5, Table 2). Observed ranges of distance moved during the trial and patterns of orientation were roughly similar to that found in males.

A total of 90 headbob displays were produced by 28 different subject animals during this study (Table 3). Although most of these displays were produced by male subjects, 11 displays were produced by 6 female subjects. More than half of the headbob displays (51) were directed towards the live animal stimulus, with the displaying lizard model receiving another quarter of the displays (23). Treatments thus differed substantially in both the number of displays produced (^{2}=55.6, df=3, $p < 0.0001$) and the number of trials in which displays were produced (^{2}=7.43, df=3, p=0.06).

Headbob displays produced during this experiment corresponded well to the displays observed for this population in the field, including almost always one A-type headbob, one or two B-type headbobs, and up to eight C-type headbobs. Displays directed at the live animal and displaying robotic lizard tended to be slightly more aggressive. For example, display-specific body postures were only directed towards the live animal (6 displays) or the displaying lizard model (2 displays), and were not observed during control trials. Directed displays were also slightly longer in duration (mean [SE] = 8.3 s [0.91] vs. 6.06 s [0.57]) and included more total headbobs (5.7 [0.60] vs. 3.8 [0.39]), but sample sizes were too small to warrant further statistical analyses.

Table 3 Number of headbob displays produced by subject animals in each treatment and number of trials in which headbob displays were produced

Treatment	Number of headbob displays observed	Number of trials in which headbob displays were observed
Experiment 1		
Empty cage	11	6
Mechanical noise	5	2
Displaying model	23	8
Live animal	51	12
χ^2	55.6 ($p<0.0001$)	7.43 ($p=0.06$)
Experiment 2		
Short, flat	26	10
Short, stilted	6	9
Long, flat	31	10
Long, stilted	22	2
χ^2	16.5 ($p<0.0001$)	5.77 ($p=0.12$)
Experiment 3		
Standard	26	7
Shudder	17	4
All doubles	26	7
All singles	17	6
χ^2	3.77 ($p=0.29$)	1.00 ($p=0.80$)

Experiment 2 – Body postures (flat versus stilted) and bob number (short versus long)

As in Experiment 1, PCA resulted in four composite variables (very similar to those described in Table 1), which together explained 70% of the variation among males. Again, MANOVA results were similar whether or not trials in which the animal did not move were included. Results below are for the full data set alone.

Male subjects were less active when presented with a stilted robotic lizard than with a flat model (Fig. 3a), leading to a significant effect of 'flat/stilted' in the MANOVA ($F=7.3$; df=1, 99; $p=0.005$; Table 2). There were no other significant differences between treatments in the other composite behavioral variables ($F<1.1$, $p>0.05$ in all cases; Table 2). Males spent more time orienting towards the short, flat and long, stilted stimuli, which correspond to the two forms of display most frequently encountered by male sagebrush lizards at this distance in the field (aggressive displays produced by both sexes, not courtship or broadcast displays). But the MANOVA interaction effect corresponding to this difference was not statistically significant (Table 2).

In contrast, females attended more to the difference between long and short displays, orienting towards short versions of the display (female aggressive and Broadcast displays) and away from the long displays typical of male courtship and aggression (Fig. 3b). The effect of bob number (but not posture) on orientation and distance from the stimulus (PC3) was statistically significant ($F=4.5$, df=1, 99; $p=0.04$, Table 2). However, because all other forms of behavior were at very low frequencies, the effect of long/short headbobs on total female behavior was not statistically significant ($F=1.9$, df=4, 93; $p=0.11$). Other forms of behavior also did not differ significantly among treatments.

In Experiment 2, only 15 of the 26 male subjects, and none of the females, produced headbobs during trials, exhibiting a total of 85 displays during the course of the experiment. Nine or ten males produced 2–3 displays each per treatment condition, except the short, stilted presentations (Broadcast displays) during which only two male subjects produced a total of 6 headbob displays (Table 3). Display structure again corresponded well to the displays observed for this population in the field, and did not differ among treatments in terms of the number of headbobs per display.

Experiment 3 – Headbob type (natural versus artificial) and pattern (single versus double bobs)

We combined measures of behavioral response in Experiment 3 into four composite variables that together explained approximately 72% of the variance, and which again were very similar in composition to the PC axes identified in the Experiments 1 and 2.

Animals were active during this experiment, moving an average of 67 cm (SE = 16.7) in each trial (compare to 40 cm [11.9] for males in Experiment 1 and 25 cm [7.9] for males in Experiment 2), perhaps having grown more accustomed to the disturbance of the experimental procedures. Nevertheless, treatment type explained very little, if any, of the variation in subject behavior in this final experiment. Subjects (all male in this experiment) spent less time producing headbob displays during the single headbob treatments (shudder and single bob; mean = 27 s [SE = 24.9] vs. 65 s [SE = 57.8]), which are rarely, if ever, directed towards males in the field. However, behavioral measures were highly variable and differences among treatments were not statistically significant when tested in MANOVAs (e.g., Table 2).

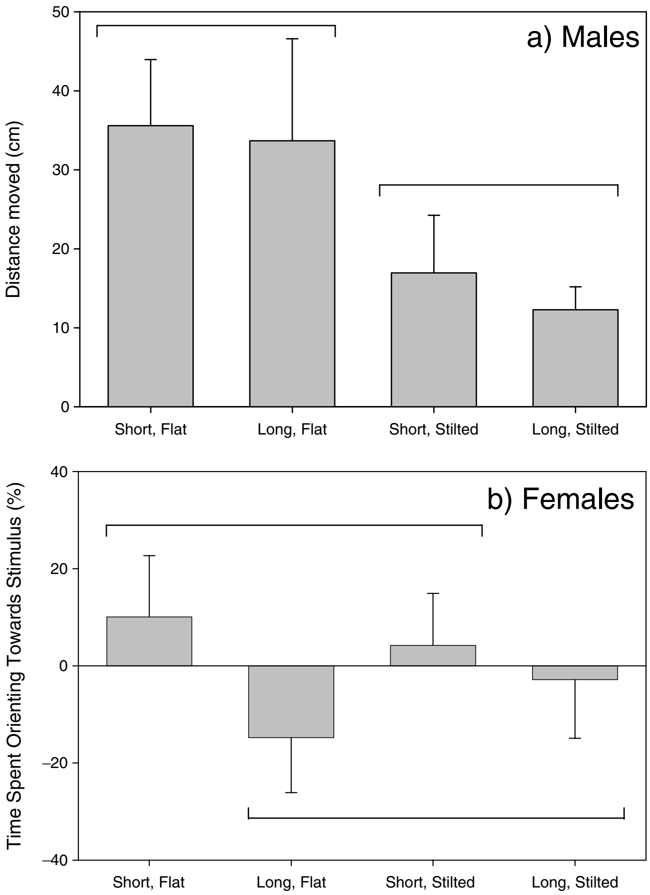

Fig. 3 Sex differences in Experiment 2 match social differences in the wild. **a** Males moved about their cages less when presented with the 'stilted' display forms typical of short-distance aggressive encounters for this species in the field. **b** Females spent a greater proportion of time orient away from the 'long, flat' displays used by males to court females and the 'long, stilted' displays indicative of aggressive encounters, but orient towards the 'short, flat' displays typical of female-female aggression. See text for details

Surprisingly, six of the lizards in this experiment produced a type of headbob display that was not observed in either of the other experiments and has not been reported for *S. graciosus* in the wild. The unusual displays were long stretches of single headbobs (BBB or BBBB) with few, if any double head-bobs (no As, but up to 3 Cs). These unusual displays were produced in 7 different trials by 6 different males, and all but one were produced the day immediately after the subject had been presented with the artificial single-bob treatment (BBBBBB). As explained in the methods, each lizard was tested with all four treatments, presented in random sequence on four consecutive days. All of the unusual displays were produced during double head-bob and standard headbob trials (identical or very similar to those used in the other two experiments), on the day immediately following the artificial single-bob treatment. The one exception was a lizard that produced BBB displays on the last day of the experiment, after having experienced all four treatment types. Headbob displays were produced in about 25% of the trials, with about the same number of lizards displaying in each treatment condition (Table 3). Slightly more headbob displays were produced in the 'double' trials (26 displays each) than in the 'single' trials (17 displays each), but this difference is not statistically significant.

Discussion

Our results support the "Multiple Receiver" rather than the "Low Cost Redundancy" hypothesis for the evolution of lizard headbob displays. Specifically, we show that male sagebrush lizard receivers are especially attentive to display-specific body postures (which distinguish the more and less aggressive displays of territorial intruders in same-sex interactions), whereas females pay more attention to the total number of headbobs in the display (which distinguish between male courtship and aggressive displays). Thus, headbob displays can be subjected to different selective pressures in different social contexts, and structural complexity in the display system may be maintained by the need to respond independently to different aspects of a complex selective regime. Because different aspects of the displays were not equally meaningful to the same display receivers, headbob displays do not appear to be consistent with the "Low Cost Redundancy" scenario (Pomiankowski and Iwasa 1993; Iwasa and Pomiankowsk 1994). And because we found significant differences in the response to some treatments, our results suggest that at least some of the complexity of the lizard headbob display is biologically meaningful, and not a statistical artifact created by human observers (as might be argued for the complexity documented in Martins 1994). Further theory is needed to consider the long-term effects of combining intra- and inter- sexual selection acting on different aspects of the same display.

Our results are consistent with other empirical studies, showing, for example, that leaf warbler color patches are more important in male competition, whereas body size is more important in female mate choice (Marchetti 1998). Similarly, male widowbirds use their colorful collars in male-male competition, but rely on their long tails as a signal to females (Andersson et al. 2002). In these other studies, however, display elements are static signals (e.g., colors and sizes) which are continuously exposed to receivers regardless of social context. Herein, we show a similar pattern for a dynamic visual signal, with components that can be turned on or off by the display producer to match the social context. Sagebrush lizards occasionally exhibit the stilted body postures without the motion of the head-bob display, and readily produce the up-and-down motion of the headbob display without the stilted body postures. Additional study is needed to determine exactly why male signalers do not signal only with the headbob pattern to females and only with body postures during same-sex aggressive interactions. Because the display can be seen from afar, signalers may be displaying to multiple receivers simultaneously. Playback experiments conducted in other contexts may also find that receivers sometimes make use of the extra information on individual, sex, and species identity contained in the headbob display.

Although traditionally described as 'core' (headbob pattern) and 'modifier' (use of body postures) components (e.g., Jenssen 1977), our results also suggest that which element is best described as "core" depends on the sex of the receiver and social context in which the display is produced, and that whether other aspects of the display actually "modify" the core signal remains to be shown. For male receivers at the short distances employed in our study, body postures (which exaggerate body size and the colorful belly patches on most *Sceloporus* lizards) appear to be at the core of the display, conveying a message of aggressive intent (see also Martins 1993). Although the Sagebrush lizard headbob pattern carries information on the species, sex, individual identity, and motivational state of displaying animals (Martins 1991, 1993), our study provides no experimental support for use of this information by male Sagebrush lizards, even as a "modifier" of the core postural signal. In contrast, for female receivers at short distances, the headbob pattern seems to be the core element, with females responding differently to short vs. long displays. Again, although we can offer no evidence that females gather information from the use of display-specific body postures, we expect that this may be due to the artificial context in which our playbacks were performed, and encourage future researchers to conduct similar playbacks in the field.

Finally, our experiments demonstrate that a robotic lizard can be used effectively in playback studies of visual display behavior in lizards, even in confined laboratory studies. Perhaps because our subjects were unable to move from one preferred perch to another or to touch and interact chemically with experimental stimuli, their behavioral response during trials was not identical to behavior observed for this population in the field (c.f., Martins 1991, 1993). For example, our subjects displayed only about half as often as animals in this population do in the wild (Martins 1991). Even the comparison between live and robotic stimuli created difficulties in interpretation. Fewer headbob displays were directed towards the robotic lizard than to the live animal – perhaps because the robotic stimulus was producing far more headbob displays than was the live conspecific and was hence perceived as being more aggressive. Nevertheless, by measuring a variety of behavioral responses, using multivariate statistics to find natural (albeit composite) units of behavior, and to conduct tests always with respect to controls, we were able to calibrate the observed responses and to interpret them meaningfully.

An interesting and unanticipated finding was that display structure is highly malleable, and that lizards both produce and respond to displays that violate the basic syntactic rules identified from field observations. When presented with artificially-created displays, several of our subject animals produced headbob displays that have never before been documented for this species, but which were similar in structure to the artificial stimulus with which they were presented. It is particularly intriguing that the unusual displays were not produced during the artificial stimulus trials, but in trials occurring at least one full day afterwards. In addition to emphasizing the importance of designing experiments which present treatments in random order, this finding suggests that even single social interactions may have long-term effects on the behavior of this territorial species. It also suggests that despite the relatively small differences between the displays produced by juvenile lizards of different ages (Roggenbuck and Jenssen 1986; Lovern and Jenssen 2003), learning may be an important component of lizard display behavior, and adult learning may be a mechanism of long-term change in the evolution of headbob displays.

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Electronic Supplementary Material

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